Discrimination Among Wave-Generated Sounds by a Swash-Riding Clam

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Abstract. Clams, *Donax variabilis*, responded to sound stimuli presented to them in a laboratory aquarium by jumping out of the sand, lying on the sand for several seconds, and digging in again. On a beach, clams jump out of the sand and ride waves, migrating shoreward with the rising tide and seaward with the falling tide. Parallels between clam behavior on a beach and that elicited in the laboratory suggest that clams cue on wave sounds to jump out of the sand. Three aspects of the response to sound were parallel. (i) Clams were most responsive to low-frequency sounds similar to those produced on a beach by waves rolling onto shore. (ii) Clams were also more responsive to louder sounds; on a beach, clams jump preferentially for the largest (loudest) 20% of waves. (iii) Responsiveness in the laboratory had an endogenous tidal rhythm, with highest activity occurring at high tide and no activity occurring at low tide; this rhythm corresponds to the activity of clams on the beach from which they were collected. By using sounds to identify large waves, clams can ride selected waves and continuously maintain position at the sea's edge as the tide floods and ebbs.

Introduction

Large populations of the coquina clam, *Donax variabilis*, migrate on sandy beaches, shoreward with the rising tide and seaward with the falling tide (as do many other clams in this genus). An individual *D. variabilis*, which can be up to 3 cm long, normally resides with the posterior edge of its shell about 2 to 7 mm under the surface of the sand. To migrate, several times each tidal cycle, it jumps out of the sand (pushing its shell upward by thrusting two to five times downward with its foot) and rides flow from

waves. This method of locomotion has been named "swash-riding" (Ellers, 1987, 1988).

Individual *D. variabilis* control where waves move them, in part, by choosing to ride specific waves (Ellers, 1995a). On a rising tide, clams jump out of the sand preferentially for the biggest waves; *i.e.*, the ones that drag them the largest distance in the shoreward direction. Astonishingly, the clams jump out of the sand before the arrival of such waves, thus effectively predicting which waves will carry them the furthest. The cues that enable this behavior have not been previously investigated.

One explanation for this discriminatory and anticipatory feat is that clams might detect sounds from waves and use differences in the character of these sounds to select waves. Sound is a reasonable candidate as a cue that enables clams to discriminate among waves because a physical mechanism linking louder sounds to larger waves is plausible. On dissipative beaches where the clams live, a breaking wave becomes a bore (a traveling cliff-like structure of tumbling water) and the bore becomes swash, which the clams ride. The higher the bore, the larger the excursion of the swash (Bradshaw, 1982). Since a higher bore has more potential energy—it has farther to fall—it tends to create more intense vibrations as water falls off its leading edge, thus emitting a louder sound. Sound is also a reasonable cue that enables clams to anticipate waves since sound travels faster than, and in front of, the bore, thus announcing its arrival. Species of *Donax* respond to sound or vibration by either jumping out of the sand or burrowing more deeply (Mori, 1938, 1950; Loesch, 1957; Turner and Belding, 1957; Tiffany, 1971; Trueman, 1971), but no quantitative data describing either wave sounds or sounds that elicited responses from clams are available.

Reports of animals using flow-induced sounds as behavioral cues are very rare. Flow-induced low-frequency sounds and infrasounds emanate from weather patterns,

topographic features, and ocean waves; such sounds can travel thousands of kilometers. Birds are able to detect infrasounds and may be able to orient relative to such features because birds can detect Doppler shifts associated with flying away from or towards infrasound sources (Kreithen and Quine, 1979). Detection of low-frequency sound and infrasound has also been shown in fish (Karlsen, 1992a, b) and cephalopods (Packard *et al.*, 1990). The function of infrasound detection in these cases is unclear, but may be related to orientation, detection of surface waves, short-term inertial guidance, or detection of low-frequency flows (Bleckmann *et al.*, 1991) from swimming motions of other fish. Avoidance of continuously vibrating sound sources in darkness has been demonstrated in herring (Blaxter and Batty, 1985).

Sound is mechanical energy (created by a vibration) that propagates through a medium as a result of kinetic and potential energy being alternately stored and released elastically by the medium. Sound propagates either through the air or through the wet beach sand at the speeds of sound in those media. As the sound vibrations travel past a point, they are detectable as temporal changes in velocity, displacement, or pressure; the latter can be measured using a hydrophone.

To determine whether listening for and distinguishing among waves is possible under the sand, I recorded wave sounds by using a hydrophone planted under the sand amidst a population of burrowed *D. variabilis*. Then, in a laboratory, I tested whether clams would respond by jumping out of the sand when wave-like sounds were presented in the absence of waves. I also used recorded wave sounds and several artificial sounds of varying loudness and frequency to test the frequency and loudness specificity of clams' responses.

The above experiments must be considered in the light of suggestions of a tidal rhythm of responsiveness to sound. Behavior of *D. variabilis* on a beach changes with time of tide (Ellers, 1995a), and jumping responses to vibration were observed during rising tides only (Turner and Belding, 1957) or during all tidal phases (Tiffany, 1971). An endogenous rhythm was suggested for *D. semigranosus* (Mori, 1938, 1950). Tidal rhythms are often found in coastal marine invertebrates, particularly in crustaceans, molluscs, and polychaetes (for a review, see Naylor, 1985). An endogenous tidal rhythm of shell gaping has been documented in a venerid clam (Williams *et al.*, 1993). Therefore, I also tested for an endogenous tidal rhythm of responsiveness to sound.

Materials and Methods

Specimens

Immediately preceding each laboratory experiment, fresh *Donax variabilis* were collected from a beach (sub-

sequently "the" beach) near Pine Knoll Shores on the seaward side of Bogue Bank, a barrier island off North Carolina. The clams were transported with sand and seawater in a thermally insulated container to the Duke University Marine Laboratory, a half-hour drive from the beach. (An insulated container is crucial; if clams heat up even slightly in transit, they subsequently show no behavioral responses.) Clams were placed in an aquarium, where they dug into sand.

General acoustic tests and analyses

Acoustic tests in the laboratory were done in a glass aquarium (50 cm long by 26 cm wide by 30 cm high) placed on a plywood table. The bottom 8 cm of the aquarium was covered with sand from the beach, and seawater was added to a depth of 28 cm.

Sounds were produced in several ways. Knocking with knuckles on the plywood table produced a low-frequency sound. In addition, sounds were produced using an underwater loudspeaker (20 cm diameter) made of polystyrene foam. The loudspeaker, located 10 cm from one end of the aquarium and partially buried in the sand, was driven by a tape recorder. Sounds played were either recorded from waves on the beach or synthesized by a sine wave generator circuit.

To determine the sound pattern reaching the clams, sounds were recorded by hydrophones buried in the sand at various locations in the aquarium. The signal from the hydrophone was amplified and digitized (8-bit resolution) at a sampling rate of 8192 Hz. This sampling rate allows detection of sounds below 4096 Hz. Higher sampling rates were unnecessary because very little sound was detected at higher frequencies when higher sampling rates were tried.

To analyze the data, several standard methods were used. Sound pressure was plotted as a function of time. The pressure functions were transformed into frequency spectra in which sound amplitude is plotted as a function of frequency. This transformation was performed using a Fast Fourier Transform (FFT) computer algorithm (Burrus and Parks, 1985, p. 107). The FFT algorithm produces a complex number for each frequency; the amplitude at each frequency interval is twice the absolute value of that complex number divided by the square root of the number of samples. Frequency resolution is the reciprocal of the time interval sampled (a 0.5-s sample of sound resolves into 2-Hz intervals).

I represented loudness of sound as either the root-mean-square (RMS) of the pressure trace over an interval of interest or as the logarithm of that value. Loudness is a subjective concept; because humans judge the relative loudness of two sounds as the ratio of their intensities, loudness is often represented using a logarithmic (decibel)

scale (Kinsler *et al.*, 1982). One conventional measure of sound levels is the intensity level (*IL*):

$$IL = 10 \log_{10}\left(\frac{I}{I_{\text{ref}}}\right) \qquad (1)$$

where I is the measured intensity and I_{ref} is a reference intensity. Intensity is the rate at which sound energy flows through a unit area. But for both plane and spherical waves,

$$I = \frac{P_e^2}{\rho c} \qquad (2)$$

where P_e = RMS sound pressure, ρ = density, and c = the speed of sound in the medium in which the sound is traveling. Although an approximate speed of sound in wet sand is obtainable from the literature, the exact speed of sound in the wet sand in the present experiment is unknown. Therefore, I present P_e rather than the derived quantity, I.

Furthermore, it is not clear, *a priori*, that clams should respond logarithmically to sound. Therefore, I present all data numerically as either pressure or P_e, but relative loudness is assumed to be represented by the ratios of the P_e values (reflected in a logarithmically transformed P_e axis in graphs that include several sounds). I also give the following conversions to a common measure called the sound pressure level, SPL:

$$SPL = 20 \log_{10}\left(\frac{P_e}{P_{\text{ref}}}\right) \qquad (3)$$

where P_{ref} = a reference pressure. For instance, a P_e of 200 Pa has an SPL of 200 dB re 1 μ Pa, whereas a P_e of 1 Pa has an SPL of 120 dB re 1 μ Pa.

Wave sounds recorded under the sand on a beach

Sounds of waves approaching the shore were recorded on the beach during several summer days. A hydrophone was buried amidst the clam population at the same depth (2–7 mm) to which these clams burrow.

The hydrophone was attached to a tape recorder that had two input-channels: one channel recorded wave sounds; the other channel simultaneously recorded an observer's verbal description of the waves. Wave sounds were thus matched with particular events in the waves. Wave sounds were plotted as pressure *versus* time or as frequency spectra calculated from 0.5-s intervals starting between 0.5 and 1 s before the arrival of swash at the hydrophone.

Tidal variation in responsiveness of clams to sounds

Clams were collected from the beach, transported to the laboratory, and placed in the aquarium. There they were exposed to natural light and dark cycles through a large window on one side of the room, but the fluorescent room lights were kept on constantly day and night to allow observation of clam behavior. About once each hour for several days, sounds were produced by knuckle knocking that was continued until no new clams emerged for 30 s. The number of clams emerging in response to each knocking stimulus was counted. A hydrophone planted in the sand in the middle of the aquarium recorded the sounds for subsequent spectral analysis. This protocol was repeated for several collections of between 100 and 170 clams each.

Collections were made on two types of days. During the first type, high tide was between noon and midnight and between midnight and noon; during the second type, high tide coincided with midnight and noon. Thus the two types of days have noon and midnight falling either in or out of phase with high tide. Comparison of temporal patterns of responsiveness on the two types of days indicates whether there is a tidal or a daily rhythm of responsiveness.

A second experiment was performed according to the same protocol except that the window was blocked off, excluding sunlight and moonlight, and the room lights were turned off except for a few seconds during sampling periods.

Clams' responsiveness to sounds from waves

Clams were collected from the beach and placed in the aquarium in front of the speaker, where they dug into the sand. Recorded sounds of waves approaching the beach (about 200 successive swash) were presented to these clams during a 45-min period starting around the time of high tide. Clam responses were observed. A hydrophone in the sand 5 cm in front of the speaker monitored the loudness of the stimuli reaching the clams. This protocol was repeated on three summer days in an experiment involving a total of 210 clams.

Frequency and amplitude specificity of responses

To test specificity of responses to sounds, I subjected clams buried in the sand in the aquarium to specific synthesized sound stimuli of different frequencies and loudnesses. Sounds were presented using the underwater loudspeaker. Sounds were (i) broadband low-frequency sound, (ii) a pure low-frequency tone (with quieter, higher frequency harmonics), and (iii) a pure high-frequency tone (with quieter, higher frequency harmonics). Each presented sound was recorded by a hydrophone buried in the sand 5 cm in front of the speaker. The RMS sound pressures (P_e) and frequency spectra were calculated.

Eighty clams were collected on the beach 30 min before high tide, transported to the laboratory, and placed hap-
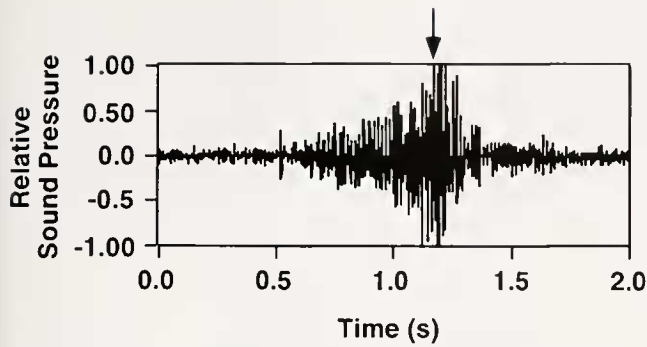
Figure 1. The sound of a wave approaching a beach as recorded from a hydrophone buried in the sand amidst the clams. Sound is represented as pressure *versus* time, with larger excursions of the pressure trace representing louder sounds. Relative sound pressure is relative to the highest pressure occurring in this trace. During the time preceding a wave's arrival at the hydrophone, a low-frequency rumble of increasing loudness is heard, culminating in a sudden increase in loudness when the wave reaches the hydrophone (arrow). Between waves there is relative silence.

hazardly in the aquarium, between the front of the speaker and the far end of the aquarium. Sounds were played to the clams during a 35-min period starting 10 min after high tide.

The sounds were presented to the clams at regular intervals (1 min silence between presentations); the signal was always of 22 ± 1 s duration. Each sound was played at a variety of intensities seven times in a row. The high-frequency signal was played first, then the broadband low-frequency signal, then the pure tone low-frequency signal. The number of clams jumping out of the sand for each stimulus was recorded. Significances of differences in responses were analyzed by regression analysis with dummy variables (Weisberg, 1980). (Statistical significance, throughout this paper, is considered to occur when the probability that the null hypothesis is true is less than 0.05.)

On two other days, additional experiments were performed according to a protocol that was identical except for the following. Instead of the three stimuli described above, a variety of synthesized low-frequency stimuli in the range of 20–100 Hz were presented. The stimuli were presented at irregular, more widely spaced intervals in random order and over a longer period of time (starting 40 min after and ending 3 h and 15 min after high tide). The number of clams responding was analyzed as a function of loudness, log (P_e), and time after high tide.

Attenuation of sound and frequency responsiveness

The results of the experiments on frequency and amplitude specificity must be interpreted relative to the frequency-specific attenuation of sound. Attenuation in the

aquarium was measured by placing a hydrophone in the sand at 4, 10, 20, 30, and 40 cm in front of the speaker. Four pure tones, covering the range of frequencies used as stimuli, were individually played by the speaker. Attenuation of sound was calculated for each as the ratio of P_e at each distance divided by P_e at 4 cm from the speaker.

Results

Wave sounds recorded under the sand on a beach

Recorded wave sounds had characteristic patterns of loudness and frequency. A bore approaching the shore made a low rumbling sound that became louder as the bore approached the hydrophone (Fig. 1). Bigger bores made louder sounds than smaller ones as they approached the hydrophone. The rumbling noise of an approaching bore consists predominantly of low frequencies ranging from 40 to 300 Hz, with the largest amplitudes being in the range of 60 to 100 Hz (Fig. 2A).

When a bore or swash reached the hydrophone, there was an additional sudden increase in loudness (arrow in Fig. 1). After a bore reached the hydrophone, the frequency content shifted toward more high-frequency components. As a bore or swash continued beachward, the sound loudness diminished.

The backwash also produced a distinct sound. It was softer than the upwash, sounded gurgly and uneven in loudness, and had more high-frequency components than swash.

Responses of clams to knocking sounds

Knocking on the plywood table under the aquarium produced a low-frequency sound with frequencies similar
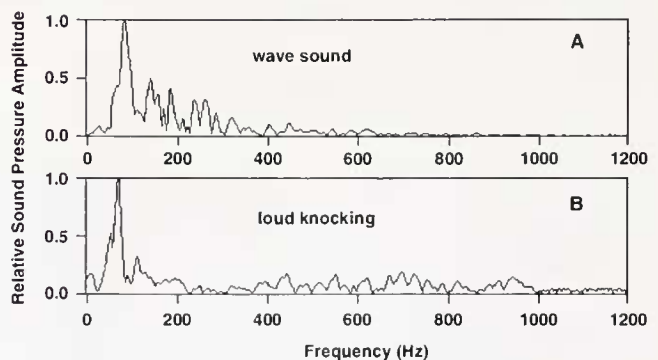

Figure 2. Comparison of frequency spectra of wave and knocking sounds that stimulate clams to jump. (A) A typical spectrum of a wave sound during a 0.5-s interval that starts between 0.5 and 1 s before swash reaches the hydrophone. The rumbling sound that precedes the arrival of swash at the hydrophone consists mainly of low-frequency components. (B) The frequency spectrum of knocking sounds presented to clams. Knocking contains low-frequency sounds similar to those which precede the arrival of swash at a spot on the beach.

to those of a bore approaching the beach (Fig. 2). *Donax variabilis* clams often responded to knocking by jumping out of the sand (Fig. 3). After a clam emerged from the sand, it fell on one valve or the other, often with siphon and foot extended. This behavior mimicked that of clams jumping out in front of swash on the beach. Clams lay on the sand for 3 to 30 s before digging in again. Occasionally, individual clams only partially emerged from the sand. Such hesitant clams could be induced to emerge completely by increasing either the loudness or the duration of knocking (suggesting that clams sum sound stimuli over time).

Tidal variation in responsiveness of clams to knocking sounds

The number of clams that jumped out of the sand depended on the time of tide, not on the time of day (Fig. 4a). Similar results were obtained when room lights were off and natural light cues were unavailable (Fig. 4b). The clams never jumped within 1 to 2 h of low tide; the number jumping increased as high tide approached, reached a maximum at high tide, and decreased after high tide. This tidal rhythm persisted in the absence of direct tidal cues (*e.g.*, the aquarium's water level did not change), and independent of the light regime provided. The tidal rhythm persisted for three to five tidal cycles; subsequently no responses to sound could be elicited.

The maximum percentage of clams jumping at a given time was only 20%. Jumping clams were not always the same individuals (individuals are recognizable by distinctive shell markings). Therefore, the 20% maximal response rate was not due merely to complete non-responsiveness in the other 80% of clams. Thus, individual clams become responsive and unresponsive several times per tidal cycle. At high tide, a larger fraction of the clams are in a responsive phase than at other times of tide.

Clams' responsiveness to sounds from waves

On all 3 days, some of the clams (maximally 20% at any given time) within a 15-cm radius of the speaker sometimes jumped out of the sand while wave sounds were being presented. In contrast, during an entire summer of observations, I never observed clams jumping in the absence of sound stimuli.

Wave sounds presented to clams consisted of naturally occurring, quiet periods several seconds long, interspersed with the rumble of incoming waves. Whereas some wave sounds elicited responses, others not obviously different elicited no responses. Because of the complex nature of wave sounds, specific features to which clams responded could not be identified unambiguously. Nevertheless, jumps often coincided with the pre-arrival rumble. The loudness, P_e, of 0.5-s samples of sound during pre-arrival
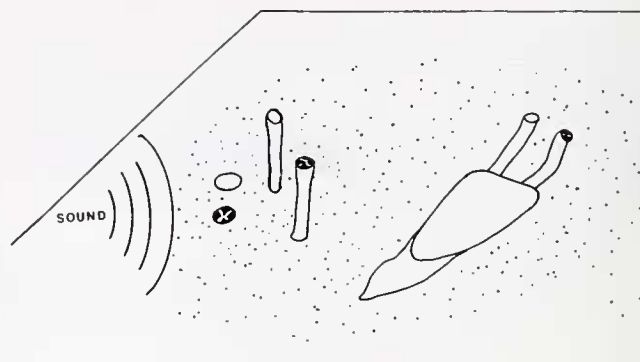
Figure 3.   Observed responses of clams to sound stimuli. In a clam that did not visibly respond, only the clam's exhalant and inhalant (frilled) siphon were visible at the surface of the sand (at left). Clams responded either by elongating their siphons (middle), usually in response to a high-frequency (832-Hz) tone, or they jumped out of the sand and lay with siphons and foot waving (at right). After 10–30 s, a clam that had jumped would again burrow into the sand.

rumbles was typically 30 Pa, which is similar to the loudness of artificial sound stimuli that elicited the responses reported below.

Frequency and amplitude specificity of responses

Two separate behavioral responses to sound were observed—siphon elongation and jumping out of the sand (Fig. 3). Siphon elongation was qualitatively noted to occur primarily in response to higher frequencies (*e.g.*, 500 and 832 Hz tones). Such elongation of the siphons was never seen in the absence of sound stimuli. This is the first report in the literature of siphon elongation as a response to sound, and its potential function is unknown.

The jumping responses were quantitatively analyzed. The frequency spectra of the sound stimuli are shown in Figure 5. At all frequencies, more clams jumped in response to louder sounds (Fig. 6). The number of clams jumping was linearly related to loudness as represented by log (P_e). For both the pure tone and the broadband low-frequency sounds, this linear relationship was tight (correlation = 0.98) and the slope was significantly non-zero ($P < 0.001$), whereas for the pure high-frequency tone, the relationship was less tight (correlation = 0.6), and the slope was not significantly different from zero ($P = 0.1$). The frequency composition did not affect responsiveness; both pure tone and broadband low-frequency sounds elicited similar numbers of clams that jumped at a given loudness (low-frequency slopes not significantly different from each other). At a given loudness, more clams jumped in response to low- than to high-frequency sounds (slopes of the low-frequency sounds were significantly higher than the slope of the high-frequency tone). No clam was ever observed jumping in the absence of a sound stimulus.
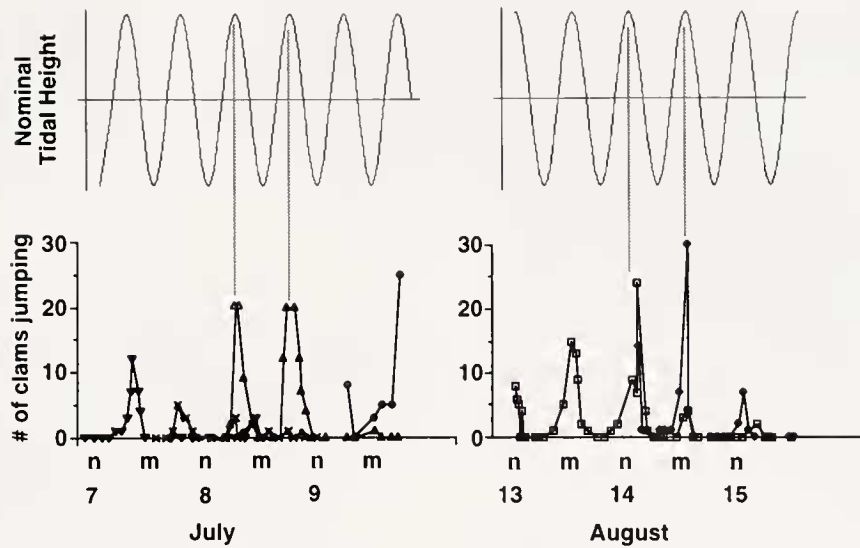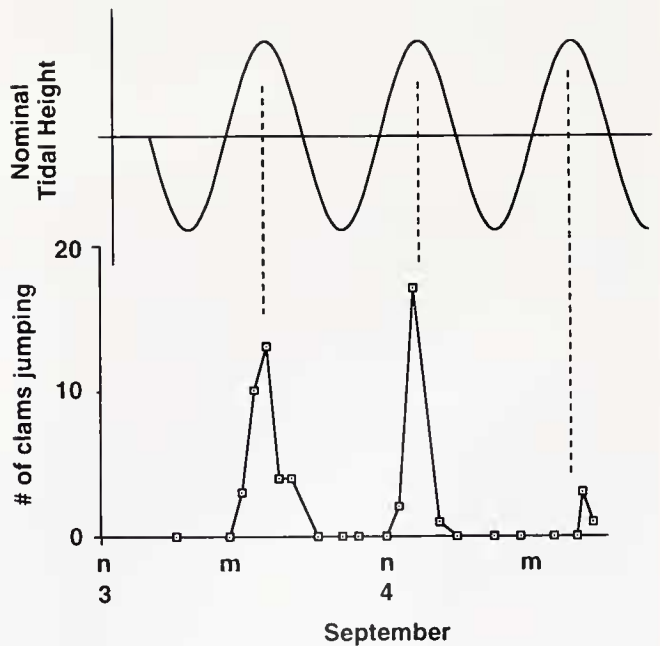
Figure 4a. Number of *D. variabilis* clams in the laboratory jumping in response to knocking sounds relative to time of day and tide. Noon is n; midnight is m. Clams were most responsive around the time of high tide and showed no response around the time of low tide. Clams responded for only three to five tidal cycles after they had been taken from the beach. The pattern shown is a compilation of several collections (represented by different symbols) taken on different days from the same beach. Room lights were continuously on in this experiment.

In the 2 additional days of experiments, performed during falling tides with several other synthesized low-frequency stimuli, jumping responses were consistent with those already described. Specifically, the number of clams responding increased with loudness, log (P_e), and decreased with increasing time after high tide (multiple regression, $P < 0.001$; loudness variable: $P < 0.01$, time variable: $P < 0.01$, $n = 35$). A cumulative total of 147 responses were observed in 35 trials during those 2 days.

On these 3 days of experiments, clams responding to sounds jumped only if they were less than 14 cm from the speaker, and most responding clams were less than 5 cm from the speaker face. The proximity of responding clams to the sound source raises the possibility of near-field effects (complicated wave interference patterns), which would complicate interpretation of the responses. A near field exists (close to a vibrating piston in an infinite baffle, an approximation to the geometry of the speaker: Kinsler *et al.*, 1982, *inter alia*) only if the diameter (0.2 m) of the speaker is greater than the sound's wavelength. For an 832-Hz sound the wavelength is 1.8 m (wavelength = speed of sound divided by frequency; speed of sound in coarse silt sea bottoms assumed = 1540 m/s; Kinsler *et al.*, 1982). The speaker is even smaller compared to the longer wavelengths of lower frequency sounds. Therefore, near-field effects are negligible in the present experiment. The spatial response pattern of clams must, however, also be considered with respect to frequency-dependent attenuation of sound.

Figure 4b. Number of *D. variabilis* clams in the laboratory jumping in response to knocking sounds relative to time of day and tide. The results are similar to those shown in Figure 4a, but in this experiment room lights were off except for a few seconds during sampling.
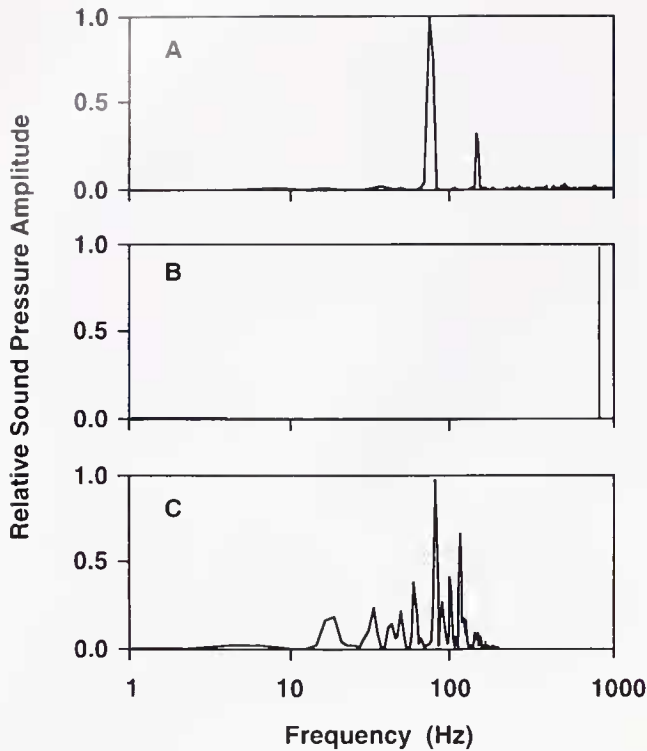
Figure 5. Frequency spectra of three artificially produced sounds presented to clams to test their responses to different sounds. The pure tone, low-frequency stimulus consisted of a 72-Hz tone with a harmonic at 144 Hz (A); the pure tone, high-frequency stimulus consisted of a 832-Hz tone (B) and a small harmonic at 1664 Hz (not shown); and the broadband, low-frequency noise had major frequency components ranging from 20 to 140 Hz (C). These frequency spectra were recorded with a hydrophone planted in the sand amidst the clams and thus represent stimuli to which the clams were exposed. Responses of clams to these sounds are shown in Figure 6.

Figure 6. Number of clams jumping in response to sounds of different loudness and frequency. Louder sounds have higher root-mean-square (RMS) pressures. Three distinct frequency spectra (Fig. 5) were presented. More clams jump at a given loudness for both broadband (20 to 140 Hz, ×) and pure tone (72-Hz, ●) low-frequency sound than for a high-frequency (832-Hz, ○) sound.

Attenuation of sound and frequency responsiveness

High frequencies attenuated more rapidly with distance from the source than did low frequencies (Fig. 7), which raises the possibility that clam responses that appeared to be frequency dependent (Fig. 6) might actually have been attenuation artifacts. The degree to which attenuation of frequency-dependent responses is contributing to the observed differential responses can be determined by considering the measured extent of attenuation in the aquarium in this experiment. Two sounds (832 and 72 Hz) of equal P_e at 4 cm from the speaker attenuated differentially; consequently, at 30 cm, the 832-Hz sound was only 10% as loud as the 72-Hz sound (Fig. 7). At 4 cm, the loudest 832-Hz stimuli were 10 times louder than the loudest 72-Hz stimuli (Fig. 6); conservatively assuming a 10% relative attenuation, at distances greater than 4 cm, the loudest 832-Hz sounds were at least as loud as the loudest 72-Hz sounds. Yet only half to a third as many clams responded to the loudest high-frequency sounds as responded to the

Figure 7. Frequency-specific attenuation of sound in the sand in the aquarium in which acoustic tests were performed (□ 832 Hz; ○ 500 Hz; × 250 Hz; + 72 Hz). The hydrophone was planted in the sand along the midline of the tank at several distances in front of the speaker. Attenuation is expressed as % RMS sound pressure at the given distance from the loudspeaker divided by RMS sound pressure 4 cm from the face of the speaker. (The slight increase in sound at the point farthest from the speaker is probably due to sound patterns caused by partial reflection of sound waves off the aquarium wall.)

loudest low-frequency sounds. Therefore, although differential sound attenuation must have contributed to the observed difference in responsiveness to different frequencies, it cannot explain the entire difference. *D. variabilis* clams are more responsive to low-frequency sounds in their jumping response.

Discussion

Wave sounds as cues for swash-riding

The proposition that *Donax variabilis* clams use sounds from waves as cues for swash-riding is supported by direct findings of responsiveness of clams to appropriate sounds and by parallels between behaviors elicited in the laboratory and observed on the beach. On the beach, these clams jump in response to waves; in a laboratory, in the absence of waves, these clams jumped in response to wave sounds and to artificially produced sounds that contained frequencies similar to those of wave sounds. Wave sounds recorded in the beach amidst coquina clams show distinct patterns of sound that allow the clams to predict the size and timing of incoming swash. For example, the loudness of a wave's sound predicts the excursion of that wave's swash. On the beach, clams preferentially jump for swash of large excursion (Ellers, 1995a); in the laboratory, clams were more responsive to louder sounds. Further correspondence between beach and laboratory is found in the observed endogenous tidal rhythm. Clams in the laboratory, which were isolated from direct tidal cues, were most responsive to sounds at high tide, and did not respond at all to sounds within 1 to 2 h of low tide. On the beach, clams did not jump out of the sand to ride waves within 1 to 2 h of low tide (Ellers, 1995a).

Taken together, these results indicate that sound is a major cue in determining whether these clams jump out of the sand to swash-ride. Loud sounds from large waves stimulate the clams to jump, and an endogenous rhythm of responsiveness modulates the jumping behavior and is thus a proximate cause of the characteristic tidal migration of these clams. This is the first report demonstrating use of flow-induced sounds by an invertebrate.

Detection of pressure or velocity signals by clams

An acoustic effect, associated with how close a responding clam is to the speaker, gives insight into possible mechanisms by which these clams may detect sounds. Sound can be detected as temporal changes in either pressure or velocity of the vibrating medium at a point. The hydrophone used in this experiment detects pressure. In contrast, organisms may use mechanisms (tiny hairs or cilia) that detect motion (velocity) rather than pressure. For a sound wave far from its source, pressure amplitude is directly proportional to velocity amplitude (Kinsler *et*

al., 1982). For sound close to its source, however, velocity and pressure are not directly proportional, and velocity attenuates more rapidly than pressure. By convention, this effect is considered important (Bobber, 1970) if the distance from the source to the receiver (hydrophone or clam) is less than half a wavelength (0.9 and 11 m for 832- and 72-Hz sounds, respectively). Therefore, in the area where the clams responded to sound, the velocity signal attenuated more rapidly than the pressure signal.

If clams had been detecting pressure, then louder sounds should have caused responses throughout the aquarium. For instance, 72-Hz sound attenuated P_e by a maximum of 50% in the aquarium (Fig. 7); therefore, a signal with twice the threshold P_e at 4 cm should have caused responses throughout the aquarium. But clams more than 15 cm from the speaker never jumped; thus, they did not jump appropriately further away when the pressure signal was increased. Since the velocity signal attenuates more with distance than the pressure signal, the locations of responding clams suggest that the animals detected velocity rather than pressure. Other more complex possibilities exist, however, regarding the transmitting medium and the sensor used. For instance, scorpions have detectors both for compressional (sound) waves under the sand and for waves traveling on the interface between air and sand (Brownell, 1984).

Population versus individual responses

Loudness and frequency were not the only factors determining whether clams jumped in response to a sound. In fact, although clams jumped in connection with specific recorded wave sounds, they ignored many waves of equal loudness. Similar indifference to otherwise suitable stimuli was also observed in the rhythm experiments; a maximum of 20% of clams responded, even at the maximally responsive times. Perhaps the responsiveness of individual clams shifts several times per tidal cycle. The relative length or frequency of the responsive periods may change with time of tide, so that a larger fraction of clams is responsive at high tide than at low tide.

Endogenous tidal rhythm

An endogenous rhythm should persist for some time in the absence of cues. In the current experiment, the tidal rhythm in responsiveness persisted without tidal cues and irrespective of potential light cues, thus supporting the endogenous nature of the tidal rhythm. But the rhythm persisted only for three to five tidal cycles under laboratory conditions, suggesting either that the rhythm is a damped oscillator or that a clock is still running but its expression is blocked. For instance, lack of food may force cessation of jumping. Such small numbers of persisting cycles are sometimes observed for tidal rhythms; *e.g.*, a tidal rhythm

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